

ETHOLOGY OF THREE COEXISTING SPECIES OF *EFFERIA*
(DIPTERA: ASILIDAE) IN MEXICO

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Abstract.—The behavior of *Efferia cressoni* (Hine), *E. subcuprea* (Schaeffer) and *E. triton* (Osten Sacken) was studied on a mountainside 80 km north in Chihuahua, Mexico. The three species were able to coexist in the same habitat because of differences in foraging/feeding sites, in time of peak foraging and in prey selection. Because they occupied different levels in the vegetation (*E. cressoni*, 5–20 cm; *E. triton*, 18 cm–1.3 m; *E. subcuprea*, 1–2 m), contact between species was apparently minimal. Although Diptera and Homoptera were primary food items, prey of different mean lengths (*E. cressoni*—5.0 mm, *E. subcuprea*—6.1 mm, *E. triton*—9.5 mm) were chosen with little overlap. Peak feeding for *E. cressoni* occurred in mid-morning and late afternoon, whereas that for *E. subcuprea* and *E. triton* occurred in mid-afternoon. These observations make a contribution to the poorly documented phenomenon of coexisting, congeneric robber flies.

According to Martin (1965), 37 species of *Efferia* (Asilinae) occur in Mexico. To our knowledge, information on the ethology and/or ecology of this genus in Mexico has been published for only one species, *E. argyrogaster* (Macquart) (Lavigne, 1979). The present study reports on the ethology and ecology of three species, (*E. cressoni* (Hine), *E. subcuprea* (Schaeffer) and *E. triton* (Osten Sacken)), which were studied primarily at Rancho Experimental "La Campana" located 80 km north of Chihuahua, during the period, April 2–11, 1972. Limited observations on *E. cressoni* were also made at the junction of Route 45 and the road to Balneario San Diego, south of Chihuahua.

Voucher specimens from populations of the asilids forming the basis for this paper have been placed in the U.S. National Museum of Natural History, Washington, D.C. as Lot #48, 49 and 50.

The habitat at "La Campana" is oak brush savannah in the foothills just below the Ponderosa Pine zone (Fig. 1). The savannah is dominated by the grasses, *Elyonurus* sp., *Aristida ternipes* Cav. and *Bouteloua gracilis* (H. B. K.) Lag. ex Steud., intermixed with red oak, *Quercus rubra* L., and two or three additional species of oak. Less common plants include *Andropogon barbinodis* Lag., *Prosopis glandulosa* Torr., *Drymaria arenaroides*, Humb. & Bonpl. ex. Roem. & Shult., *Brikelia spinuloso* Gray and *Nolina texana* Wats.

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METHODS

Methods for gathering and analyzing ethological data for this study were essentially the same as those described for *Neoitamus vittipes* (Macquart) in Lavigne (1982).

ETHOLOGY OF INDIVIDUAL SPECIES

Efferia cressoni

Foraging and feeding behavior.—*Efferia cressoni* foraged from soil, rocks and vegetation (5 to 20 cm above the ground), depending on the surface temperature of the substrate. Usually this species foraged from the ground until the surface temperature reached 41°C, but some individuals waited until the temperature reached 48°C before moving onto vegetation. Once the asilids moved to vegetation they generally foraged from shaded areas.

This species exhibited positional changes in relation to the sun while resting on the ground. In the morning and late afternoon when surface temperatures varied between 24 and 37°C, individuals generally oriented themselves broadside to the sun. As the surface temperature increased, they turned to face directly into the sun.

Efferia cressoni captured prey in flight. Forage flights usually covered a distance of 1 m or less. Five to eight flights were frequently made before prey were captured.

Intermittently during feeding (Fig. 2), as has been observed for most *Efferia* spp., the asilid hovered and manipulated its prey with all six tarsi prior to reinserting its hypopharynx. Two incomplete feedings were observed to last 11 (Cixiidae: *Oecleus* sp.) and 15.5 minutes (prey unidentified); one complete feeding lasted 18 minutes (Scythridae: *Scythris* sp.). At the completion of feeding, prey were pushed off the hypopharynx with the foretarsi while the asilid was still at the feeding site or prey were dropped in flight as the asilid resumed foraging.

The following is a list of prey taken by *E. cressoni*. The number and sex of the predator are indicated in parentheses following the recorded prey.

COLEOPTERA, Anthicidae: *Anthicus* sp., IV-8-72 (♂); Cleridae: *Phyllobaenus discoideus* (LeConte), IV-8-72 (♀); Scarabaeidae: *Aphodius vittatus* Say, IV-6-72 (♀). DIPTERA, Agromyzidae: *Calycomyza* sp., IV-11-72 (♀); *Liriomyza* sp., IV-8-72 (♀); Anthomyiidae: *Hylemya* sp., IV-4-72 (♀), IV-5-72 (♀); Asilidae: *Efferia cressoni* (Hine), IV-8-72 (♀); Bombyliidae: *Lepidanthrax proboscideus* (Loew), IV-11-72 (♀); *Mythicomyia* sp., IV-8-72 (♂); Cecidomyiidae: *Neolasioptera* sp., IV-8-72 (♀), IV-11-72 (♀); unidentified, IV-8-72 (♂,♀); Chloropidae: *Conioscinella* sp., IV-8-72 (♀); Muscidae: *Limnophora* sp., IV-5-72 (♀); *Orthellia caesarion* (Meigen), IV-6-72 (♀); Sarcophagidae: *Blaesoxipha* sp., IV-6-72 (♀); Tachinidae: *Mochlosoma* sp., IV-9-72 (♀); Tephritidae: *Trupanea wheeleri* Curran, IV-6-72 (♀), IV-8-72 (♂), IV-11-72 (♀). HEMPTERA, Lygaeidae: *Crophius heidemanni* Van Duzee, IV-6-72 (♂); *Geocoris* sp., IV-5-72 (♀); Rhopalidae: *Niesthrea sidae* (Fabricius), IV-9-72 (♀); Tingidae: *Gargaphia opacula* Uhler, IV-5-72 (♀). HOMOPTERA, Aleyrodidae: unidentified, IV-9-72 (♂), IV-11-72 (♀); Aphididae: *Arytainia* sp., IV-9-72 (♀), IV-11-72 (2 ♀); *Macrosiphum* sp., IV-8-72 (♀), IV-9-72 (♀); Cicadellidae: *Balclutha* sp., IV-8-72 (♀); *Deltocephalus sonorus* Ball, IV-11-72 (♀); *Dikraneura* sp., IV-8-72 (♂,♀); *Exitianus exitiosus* (Uhler), IV-8-72 (♀); *Norvellina* sp., IV-8-72 (♂); *Stirellus obtutus* (Van Duzee), IV-8-72 (♀); *Texananus pergradus*



Figs. 1-7. 1, Overview, "Rancho Campana," *Efferia* habitat. 2, Female *E. cressoni* feeding on *Hylemya* sp. 3, Cannibalism by female *E. cressoni*. 4, *E. cressoni* pair in copula. 5, *E. cressoni* female ovipositing in *Bouteloua* sp. seed head. 6, Eggs of *E. cressoni*. 7, *E. subcuprea* female feeding on *Geocoris* sp.

Table 1. Comparison, by number and percent, of the composition of prey, by Order, taken by *Efferia cressoni*, *E. subcuprea* and *E. triton*.

Order	Male						Female						Total									
	<i>E. cressoni</i>		<i>E. subcuprea</i>		<i>E. triton</i>		<i>E. cressoni</i>		<i>E. subcuprea</i>		<i>E. triton</i>		<i>E. cressoni</i>		<i>E. subcuprea</i>		<i>E. triton</i>					
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%				
Arenaeae	1	8.3			8	19.0							1	5.9			6	14.0	3	5.5	14	16.5
Colcoptera	3	25.0	1	50.0	17	40.5	17	39.5	7	41.2	12	27.9	20	36.4	8	42.1	29	66.4	29	66.4	29	34.1
Hemiptera	1	8.3			7	16.7			1	5.9	5	11.6	4	7.3	1	5.3	12	27.9	4	7.3	12	14.1
Homoptera	5	41.7	1	50.0	15	34.9	6	35.3	6	35.3	2	4.7	20	36.4	7	36.8	2	4.7	20	36.4	2	2.4
Hymenoptera	1	8.3			3	7.1					9	20.9	1	1.8			9	20.9	1	1.8	12	14.1
Lepidoptera	1	8.3			6	14.3			1	5.9	5	11.6	6	10.9	1	5.3	11	25.2	6	10.9	11	12.9
Neuroptera					1	2.4			1	5.9	3	7.0			1	5.3	4	9.3	3	7.0	4	4.7
Orthoptera											1	2.3					1	2.3			1	1.2
Unidentified																						
Total	12		2		42		43		17		43		55		19		85		85		85	

Table 2. Comparison of relation between length of asilids and that of their prey for *Efferia cressoni*, *E. subcuprea* and *E. triton*.

Species by Sex	Predator Length (mm) ^a			Prey Length (mm)			No. of Prey Measured	Mean Ratio of Predator to Prey
	Minimum	Maximum	Mean	Minimum	Maximum	Mean		
<i>Efferia cressoni</i> ♂	11.4	14.2	12.8	0.5	10.7	5.9	10	2.2
<i>Efferia cressoni</i> ♀	11.3	15.0	13.4	1.1	13.5	4.3	37	3.1
Species mean			13.1			5.0		2.6
<i>Efferia subcuprea</i> ♂	15.3	17.7	16.4	4.8	4.8	4.8	1	3.4
<i>Efferia subcuprea</i> ♀	15.8	20.4	19.1	1.5	8.7	6.2	14	3.1
Species mean			17.9			6.1		2.9
<i>Efferia triton</i> ♂	16.7	23.5	20.9	2.8	20.0	10.2	38	2.0
<i>Efferia triton</i> ♀	21.8	26.0	23.8	2.5	26.5	8.9	43	2.7
Species mean			22.3			9.5		2.3

^a 10 predators of each were measured.

(DeLong), III-7-72 (♀) (Jct. Rte. 45 and Balneario San Diego); Cixiidae: *Oecleus* sp., IV-6-72 (♀); Delphacidae: *Bostaera* sp., IV-6-72 (♀); Issidae: *Aphelonema* sp., IV-8-72 (♂,♀); Psyllidae: *Craspedolepta pulchella* Crawford, IV-8-72 (♂), HYME-NOPTERA, Anagymini, IV-8-72 (♀). LEPIDOPTERA, Gelechiidae: *Gnorimoschema* sp., IV-8-72 (♀); *Sophronia* sp., IV-8-72 (♀), IV-9-72 (♀); Olethreutidae: unidentified, IV-2-72 (♀); Pyralidae: Peoriinae, IV-8-72 (♀); Scythridae: *Scythris* sp., IV-6-72 (♀). Unidentified: IV-6-72 (♀).

As indicated in the prey list, a female *E. cressoni* was observed preying on another female. This asilid species also was preyed upon occasionally by *E. triton* (Fig. 3).

Both sexes of *E. cressoni* generally fed on the same orders of prey, with Diptera and Homoptera making up at least 66 percent of the prey (Table 1). However, males fed on slightly larger prey, as indicated by a smaller mean ratio of predator to prey (Table 2). Overall this species was 2.6 times as large as its prey.

Mating behavior.—Male *E. cressoni* performed searching flights for receptive females with which to mate. Males weaved in and out of the vegetation, flying approximately 5 to 30 cm above the ground. During these flights males attempted to mate with females as well as with other males.

Only two complete matings were observed. Both matings were initiated in flight. The male grasped the female on the dorsum of her thorax and the struggling pair fell to the ground where the male proceeded to clasp the female's genitalia. The mated pair then flew onto vegetation, 60 cm above the ground.

During copulation *E. cressoni* remained in the male over female position (Fig. 4) as did *E. subcuprea* and *E. triton*. While in this position the male's abdomen curved around to the right or left of the female's abdomen and clasped her genitalia from below. The male's and female's wings were generally spread at a 30 to 45 degree angle to their bodies (one male was observed with his wings closed over his dorsum). The male's foretarsi rested on the female's eyes.

As mating neared completion, (within 1 to 2.5 minutes), males frequently briefly buzzed their wings. Then, just before termination, males buzzed their wings again, moved to the female's side and pushed off with all six legs.

The two observed complete matings lasted 7 and 7.5 minutes. Temperatures at mating heights (40 cm and 80 cm) were 27.2°C and 29.4°C, respectively. An additional pair already in copula when first observed, remained so for six minutes on a thornbush branch 40 cm above the substrate.

Oviposition behavior.—Female *E. cressoni* oviposited 18 to 30 cm above the ground in *Bouteloua* sp. seed heads (Fig. 5), and between the sheath and stem of the stalks. While searching for a suitable site to deposit eggs and during oviposition, females oriented in a head-up position. Ovipositions, at temperatures of 33–34°C, were completed in 45 to 60 seconds once a suitable location was found.

After ovipositing, females searched for another oviposition site or began foraging. Followed females oviposited at least twice before initiating foraging or being lost to sight.

Females deposited 2 to 5 eggs per oviposition. All eggs were oval and creamy-white (Fig. 6). Eggs ranged in length from 1.36 to 1.45 mm (\bar{x} 1.41 mm). The range in width was 0.51 to 0.57 mm, with a mean of 0.54 mm.

Daily rhythm of activity.—*Efferia cressoni* foraged/fed throughout the day; however, peak periods occurred during the morning (1000 to 1100 h) and early evening (1800 to 1900 h), i.e. during cooler parts of the day (Fig. 14). These foraging periods generally corresponded with or preceded the peak mating and oviposition periods, possibly because of the large amount of energy required for the latter behaviors. Also, during the peak foraging periods more prey were in flight and *E. cressoni* could backlight the prey making them more readily visible. During peak behavior periods, the air temperature 15 to 40 cm above the ground, varied between 27 and 34°C.

Efferia subcuprea

Foraging and feeding behavior.—*Efferia subcuprea* usually foraged from vegetation, in particular *Quercus* sp., 1 to 2 m above the ground, although some individuals were observed foraging as high as 3 m. This species was rarely observed foraging from the ground (i.e. soil, rocks, sticks).

Whether on ground or vegetation, *E. subcuprea* adjusted its body to temperature changes. In the early morning and late afternoon-evening when it was relatively cool, the asilids flattened themselves against the substrate and/or oriented their bodies broadside to the sun. During warmer parts of the day they faced the sun with their bodies held off the substrate.

Efferia subcuprea often initiated foraging flights from the same branch several times in succession. Generally, the asilids faced into the sun so that potential prey were backlit. Forage flights covered distances up to 18 to 24 cm, but most prey were captured 60 cm to 15 m from the foraging site.

Prey were always captured in flight. If they were deemed unsuitable, they were released following manipulation with all six tarsi as the asilid hovered. Acceptable prey were generally immobilized in flight immediately following capture or as the asilid hovered and manipulated the prey. The hypopharynx was usually initially inserted in the prey's head or between the head and thorax (Fig. 7). However, one asilid was observed inserting its hypopharynx in the prey's thorax after landing to feed.

During feeding prey were manipulated either, (1) with all six tarsi as the asilid



8



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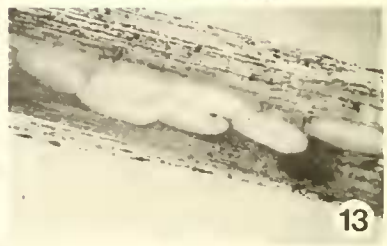
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Figs. 8-13. 8, *E. subcuprea* pair in copula. 9, *E. triton* male feeding on *Sandia macfarlandi*. 10, *E. triton* pair in copula. 11, *E. triton* male separating from female. 12, *E. triton* female ovipositing on grass stem. 13, Eggs of *E. triton*.

hovered above its feeding site, or (2) with the foretarsi as the asilid remained on its feeding site.

One complete feeding on *Hippelates robertsoni* Sabrosky (Diptera: Chloropidae) lasted 4 minutes. This was followed by a 1 minute interfeeding time after which the asilid captured another prey and was lost to sight.

At the completion of feeding, prey were discarded in one of two ways: (1) they

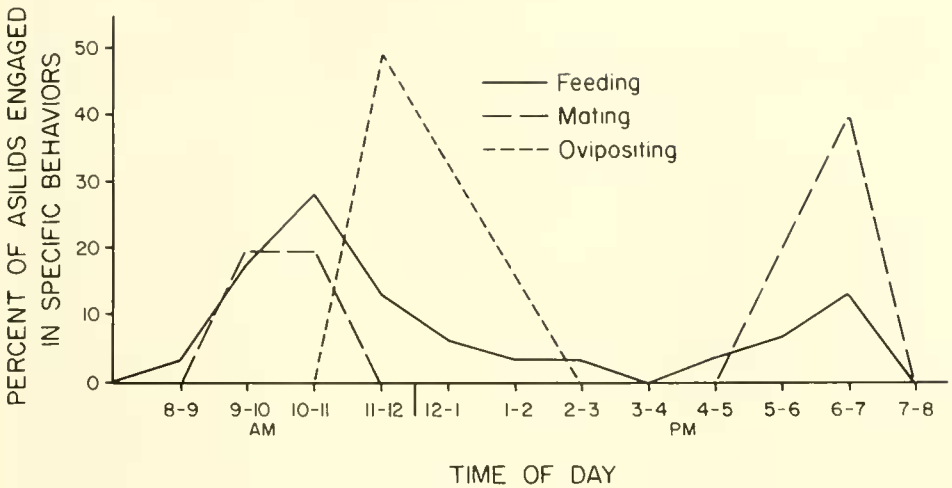


Fig. 14. The diurnal rhythm of activity of *Efferia cressoni*. (The percentage of asilids engaged in specific behavior patterns was calculated from the total number of observations for each behavior—60, 5, and 6 for feeding, mating and oviposition, respectively).

were either dropped in flight as the asilid moved to another location and/or resumed foraging, or (2) they were pushed off the asilid's hypopharynx with the foretarsi while the asilid remained at the feeding site.

Only 19 prey were recovered from captured *E. subcuprea*, as follows: ARANEIDA, Araneae: unidentified, IV-6-72 (♀). DIPTERA, Chloropidae: *Hippelates robertsoni* Sabrosky, IV-5-72 (2 ♀), IV-11-72 (♀); Drosophilidae: *Sinophthalmus pictus* Coquillett, IV-3-72 (♀); Phoridae: *Megaselia* sp., IV-9-72 (♀); Sarcophagidae: *Ravinia lherminieri* (Robineau-Desvoidy), IV-4-72 (♀); Sepsidae: *Sepsis neocynipsea* Melander and Spuler, IV-2-72 (♀); Tephritidae: *Trupanea ageratae* Benjamin, IV-4-72 (♂). HEMIPTERA, Lygaeidae: *Geocoris* sp., IV-3-72 (♀). HOMOPTERA, Cixiidae: *Oecleus* sp., IV-10-72 (♀); Membracidae: *Cyrtolobus* sp., IV-11-72 (♂); Psyllidae: *Kuwayama medicaginis* (Crawford), IV-4-72 (2 ♀), IV-8-72 (♀), IV-10-72 (♀), IV-11-72 (♀). LEPIDOPTERA, Olethreutidae: unidentified, IV-6-72 (♀). NEUROPTERA, Chrysopidae: *Eremochrysa punctinervis* (McLachlan), IV-2-72 (♀).

As can be seen from Table 1, *E. subcuprea* like *E. cressoni*, preyed primarily on Diptera and Homoptera. These two orders made up approximately 80 percent of the prey of *E. subcuprea*.

Since it was possible to measure only one prey for a male, it is difficult to say anything about the mean ratio of predator to prey for males (Table 2). Females were approximately 3 times as large as their prey.

Mating behavior.—Three mating pairs of *E. subcuprea* were observed. Of these, two complete matings were recorded to last 6.5 minutes. Temperatures during matings ranged from 24–30°C.

Mating occurred in the male over female position following initiation in flight. The male's abdomen curved around to the right or left of the female's abdomen and his genitalia clasped her genitalia from below (Fig. 8). The male's foretarsi

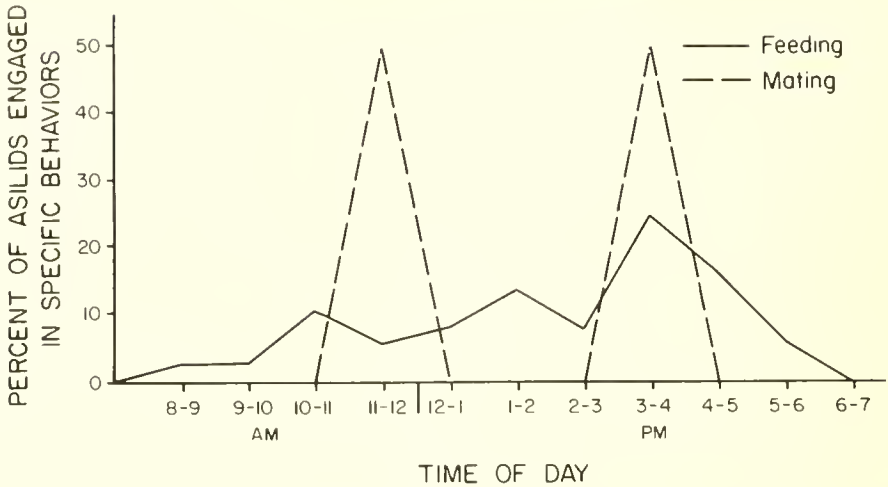


Fig. 15. The diurnal rhythm of activity of *Efferia subcuprea*. (The percentage of asilids engaged in specific behavior patterns was calculated from the total number of observations for each behavior—36 and 2 for feeding and mating, respectively).

rested on the female's eyes and his wings were closed over his dorsum. The female's wings were at a 45 degree angle to her body.

The male of one mating pair was observed to palpate the female's abdomen with his hindtarsi 1.5 minutes before the termination of mating. In addition, for 30 seconds prior to the termination of mating, the male intermittently buzzed his wings.

Mating was terminated by the male climbing up on the female or falling to one side and then pushing off with all six tarsi.

Oviposition behavior.—Female *E. subcuprea* were not observed ovipositing. However, because this species spends most of their time on *Quercus* sp. and since females have long, laterally flattened ovipositors, cracks and crevices in the tree bark or seed heads of composites probably serve as oviposition sites.

Daily rhythm of activity.—*Efferia subcuprea* foraged/fed at a fairly constant level throughout the day, beginning between 0800 and 1000 h and continuing to 1700 to 1800 h. (Fig. 15). The peak observed feeding period occurred between 1500 and 1600 h.

One observed mating occurred simultaneously with the peak feeding period, whereas another mating occurred in the morning between 1100 h and 1200 h.

Efferia triton

Foraging and feeding behavior.—As was observed for *E. cressoni*, *E. triton* foraged from both the ground and vegetation (18 cm to 1.3 m above the ground), depending upon the temperature of the ground surface. This species usually foraged from the ground, including rocks, until the surface temperature reached 37 to 39°C. Some asilids remained on the ground until the temperature reached approximately 49°C, however at that temperature their foretarsi were elevated above their heads.

Efferia triton also has developed additional behaviors to adapt to temperature

variations. During cooler parts of the day when the surface temperature was 32 to 36°C or less, the asilids would flatten themselves against the ground with their broadside to the sun. As substrate temperatures increased they lifted their bodies high above the substrate and faced into the sun.

As *E. triton* foraged, it made several round trip flights from a single location. Generally flights were initiated every 15 to 90 seconds covering distances of 15 cm to 2.5 m. This species successfully captured prey at these distances. Other species of Asilidae which we have observed usually capture prey at shorter distances than those over which they forage. This observation suggests that *E. triton* may have better vision than some other asilid species. Melin (1923) also noted differences in the visual acuity of the species that he studied.

When this species changed foraging positions, it flew 3 to 4 m in and out of the vegetation, 3 to 4 cm above the ground. If the wind blew in excess of 16 to 19 km/h the asilids minimized all activity and flattened themselves against the surface upon which they were resting.

As was observed for the other two species of *Efferia*, *E. triton* was most successful when the prey was backlighted. Melin (1923) also noted that, “. . . robberflies often catch their prey against the sun”

Efferia triton caught most of its prey in the air although one female attacked and captured an unidentified grasshopper nymph clinging to a grass stem. Following prey capture, the asilids would often hover and manipulate the prey with all six tarsi. Unsuitable prey were then released, whereas the asilids inserted their hypopharynx in the dorsum of the head, thorax or abdomen of acceptable prey. During the feeding process abdomens were typically pierced last (Fig. 9).

Intermittently during feeding *E. triton* would hover above its feeding site and manipulate prey with all six tarsi prior to reinserting its hypopharynx. This behavior often occurred two to four times as the asilids fed. One female manipulated a prey by falling on her side and using all six tarsi to reposition the prey prior to reinserting her hypopharynx.

Efferia triton fed on prey for periods ranging from 2 to 40 minutes (\bar{x} 14 min.). There was a positive correlation between prey length and the time spent feeding. Prey with an average length of 6.8 mm (e.g. Hymenoptera: Anthophoridae, *Ceratina* sp.) were fed on for approximately 5.5 minutes. Larger prey, such as *Ravinia lherminieri* (R.-D.) (Diptera: Sarcophagidae) with an average length of 9.8 mm, were fed on for an average of 30 minutes.

At the completion of feeding, prey were pushed off the asilid's hypopharynx with the foretarsi while the asilid was at the feeding site or prey were dropped in flight as the asilid resumed foraging and/or moved to a new location.

This species has an interfeeding time of 4 to 12 minutes, (\bar{x} 7.5 min.). These interfeeding times are relatively short when one considers the large size of the prey which *E. triton* captures. Asilids of similar size which feed on prey similar in size to that of *E. triton* usually have longer interfeeding times (Dennis and Lavigne, 1976, 1979).

The following is a list of prey taken by *E. triton*: COLEOPTERA, Bruchidae: *Zabrotes* sp., IV-9-72 (♂); Chrysomelidae: *Coscinoptera mucorea* (LeConte) or near, IV-11-72 (♀); *Pachybrachys* sp., IV-5-72 (♂), IV-8-72 (♂), IV-11-72 (♀); Scarabaeidae: *Anomala* sp., IV-2-72 (2 ♂, ♀), IV-3-72 (♂,♀), IV-4-72 (♀), IV-5-72 (♂), IV-9-72 (♂,♀). DIPTERA, Asilidae: *Efferia cressoni* (Hine), IV-2-72 (♂), *Efferia*

subcuprea (Schaeffer), IV-8-72 (♂), IV-9-72 (2♂), IV-10-72 (♂), IV-11-72 (2♂); Bombyliidae: *Lepidanthrax proboscideus* (Loew), IV-6-72 (♂); *Lordotus apicula* (Coquillett), IV-11-72 (♀); *Lordotus divisus* Cresson, IV-6-72 (♀), IV-11-72 (♂); Calliphoridae: *Phormia regina* (Meigen), IV-3-72 (♂), IV-8-72 (♂,♀), IV-9-72 (♀), IV-10-72 (♀); Cecidomyiidae: *Neolasioptera* sp., IV-9-72 (♀); Chloropidae: *Thaumatomyia* sp., IV-9-72 (♀); Sarcophagidae: *Ravinia lherminieri* (Robineau-Desvoidy), IV-2-72 (♀), IV-4-72 (♀), IV-9-72 (♀); Scenopinidae: *Scenopinus* sp., IV-9-72 (♂); Stratiomyiidae: *Pachygaster* sp., IV-9-72 (♂); Syrphidae: *Eristalis latifrons* Loew, IV-10-72 (♀); Tachinidae: *Olenochaeta kansensis* Townsend, IV-11-72 (♂), *Paradidyma singularis* (Townsend), IV-10-72 (♀); *Peleteria* sp., IV-11-72 (♂); unidentified, IV-11-72 (♂); Tephritidae: *Trupanea actinobola* (Loew), IV-10-72 (♂). HEMIPTERA. Alydidae: *Alydus eurinus* (Say), IV-10-72 (♂); *Stachyocnemus apicalis* (Dallas), IV-9-72 (♂); Cydnidae: *Cydnoides renormatus* (Uhler), IV-6-72 (♂), IV-9-72 (♀); Lygaeidae: *Xyonysius californicus* (Stål), IV-3-72 (♂); Miridae: *Neurocolpus nubilis* (Say), IV-10-72 (♂); Pentatomidae: *Thyanta pallidovirens* (Stål), IV-2-72 (♂); *Trichopepla* sp., IV-6-72 (♀); Rhopalidae: *Arhyssus lateralis* (Say), IV-8-72 (♀), IV-9-72 (♀); Scutelleridae: *Homaemus parvulus* (Germar), IV-3-72 (♂), IV-10-72 (♀). HOMOPTERA. Cixiidae: *Oecleus* sp., IV-10-72 (♀); Membracidae: *Ophiderma* sp., IV-9-72 (♀). HYMENOPTERA. Anthophoridae: *Ceratina* sp., IV-2-72 (♀); Apidae: *Apis mellifera* L., IV-11-72 (2 ♀); Ichneumonidae: *Anomalon* sp., IV-10-72 (♀); *Carinodes* sp., IV-5-72; *Coccygomimus* sp., IV-5-72 (♀); unidentified, IV-9-72 (♀); Pompilidae: *Agenioideus birkmanni* (Banks), IV-11-72 (♀); Sphecidae: near *Tachysphex* sp., IV-3-72 (♀), IV-8-72 (♂); *Tachysphex* sp., IV-3-72 (♂), IV-11-72 (♂). LEPIDOPTERA. Gelechiidae: *Eudactylota* sp., IV-6-72 (♂); *Filatima albilorella* (Zeller), IV-9-72 (♀); prob. *Filatima* sp., IV-6-72 (♀); Geometridae: *Semiothisa californiaria* (Packard), IV-9-72 (♀); Lycaenidae: *Hemiargus isola alce* (W. H. Edwards), IV-9-72 (♂); *Sandia macfarlandi* Clench and Miller, IV-3-72 (♀), IV-4-72 (♂); Noctuidae: *Bulia* sp., IV-9-72 (♂); Pieridae: *Nathalis iole* Boisduval, IV-6-72 (♂); Pyralidae: Peoriinae, IV-10-72 (♀), *Pyrausta perrubralis* (Packard), IV-8-72 (♂). NEUROPTERA. Chrysopidae: *Eremochrysa punctinervis* (McLachlan), IV-10-72 (2 ♀), IV-11-72; Myrmeleontidae: *Brachynemurus sackeni* Hagen, IV-11-72 (♀). ORTHOPTERA. Acrididae: *Psoloessa texana pusilla* (Scudder), IV-2-72 (♀).

As can be seen from the prey list, *E. triton* preyed on both male and female *E. cressoni* and *E. subcuprea*. Since only male *E. triton* were observed preying on these species, they may have been initially trying to mate. As was observed for *Machimus callidus* (Williston) (Dennis and Lavigne, 1979), male *E. triton* may need to make contact with another asilid before being able to determine its suitability as a mate. In addition, prey size and movement stimulate both foraging and mating.

Efferia triton fed primarily on Diptera, which comprised approximately 34 percent of the prey (Table 1). Coleoptera, Hemiptera and Hymenoptera each made up about 14 to 17 percent of the prey, respectively, followed by Lepidoptera, Neuroptera, Homoptera and Orthoptera. Male and female *E. triton* exhibited similar food choices. Males fed mainly on Diptera while females fed on both Diptera and Hymenoptera.

This species was 2.3 times as large as its prey (Table 2). Females fed on smaller prey than did males and thus had a larger predator to prey ratio.

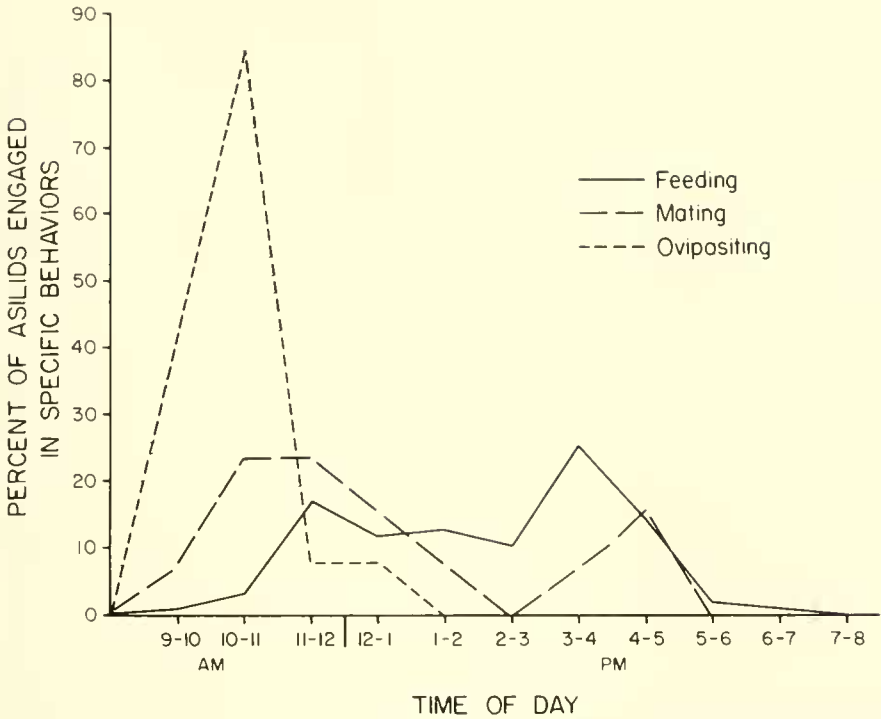


Fig. 16. The diurnal rhythm of activity of *Efferia triton*. (The percentage of asilids engaged in specific behavior patterns was calculated from the total number of observations for each behavior—115, 13 and 13 for feeding, mating and oviposition, respectively).

Mating behavior.—Male *E. triton* exhibited searching flights for receptive females with which to mate. These flights covered 5 to 10 m during which the males often buzzed their wings.

Matings were ordinarily initiated in flight, although one mating was initiated when a male landed on a female resting on the vegetation. Additionally, males could be stimulated to chase and mate by releasing females in their vicinity.

The mating sequence and position taken (Fig. 10) was similar to that observed for *E. cressoni* and *E. subcuprea*. However, matings lasted for only 45 to 90 seconds, with an average of 61 seconds. As mating neared completion the male generally buzzed its wings continuously for 5 to 30 seconds, then fell to the females' right or left side and used all six legs to separate (Fig. 11). One male buzzed his wings during the entire 45 second mating. Another male buzzed his wings for 28 seconds, stopped, and then buzzed another 8 to 10 seconds before separating from the female.

Once copulated *E. triton* moved onto vegetation 7.5 cm to 2.5 m above the ground. The air temperature at the height of mated pairs varied between 25 and 34°C (\bar{x} 29.6°C).

Oviposition behavior.—*Efferia triton* females oviposited 10 to 30 cm above the ground between the sheath and stem of dead grass stalks (Fig. 12), dead Asteraceae (Compositae) and *Nolina texana* (Lilaceae) stems. While searching for

a suitable site to deposit eggs, each female crawled up and around vegetation probing with its ovipositor.

Females deposited 3 to 13 eggs per oviposition with an average of 7 eggs, over a 35 second to 2 minute period. Eggs were oval and creamy-white (Fig. 13). Ninety-four eggs were measured which ranged in length from 1.48 to 1.87 mm (\bar{x} 1.72 mm) and width and from 0.43 to 0.71 mm (\bar{x} 0.58 mm).

Following an oviposition, females would begin searching for another oviposition site or forage. Females oviposited from 5 to 12 times before initiating foraging or being lost to sight. Temperatures at heights where ovipositing females were encountered varied from 29–36°C.

Daily rhythm of activity.—*Efferia triton* also foraged/fed throughout the day (Fig. 16). However, this species exhibited two peak foraging periods one between 1100 and 1200h and the other between 1500 and 1600 h.

Mating *E. triton* were observed mainly between 1000 h and 1200 h. However, another peak period occurred between 1600 and 1700 h. Oviposition also took place mainly in the morning between 1000 and 1100 h.

Since the peak foraging/feeding periods generally followed mating and oviposition, this species was probably replenishing the energy expended during these activities.

SPECIES COEXISTENCE

Limited information has been published on factors that potentially allow several species of Asilids to coexist in a given habitat. Thus, it is of interest to examine the data presented in this paper and speculate on the factors which might allow the three congeneric species to coexist.

Because limited data are presented for some behaviors, especially those for *E. subcuprea*, it is not possible to consider all factors which may be important. The available pertinent data concerns: (1) foraging/feeding sites, (2) prey type, (3) foraging times, and (4) predator and prey length.

All three species foraged and fed at different elevations in the vegetation, with very little overlap. *Efferia cressoni* utilized the microhabitat 10 to 15 cm above the ground. Both *E. triton* and *E. subcuprea* foraged higher in the vegetation, 18 cm to 1.3 m and 1 to 2 m above the ground, respectively. Lehr (1969), in Russia, also noted that asilids utilize different levels in a habitat ("hunting zones") and thus partition resources. This strategy minimizes competition between asilids in a habitat. Lehr also observed that the Asilinae show a more distinct layering of hunting zones than do the Dasypogoninae.

Because *E. cressoni*, *E. triton* and *E. subcuprea* foraged and fed at different levels in the vegetation, one might expect them to feed on different prey. However, examination of Tables 1 and 2 show that the three species exhibited high overlap in terms of insect orders taken. *Efferia cressoni* and *E. subcuprea* fed predominantly on Diptera (36, 42%) and Homoptera (36, 37%), whereas *E. triton* fed mainly on Diptera (34%). Conversely, a close examination of the prey lists shows that these species exhibited very little overlap at the genus and species levels. Each species presumably fed on prey which inhabited their foraging levels. Dennis and Lavigne (1976) have previously observed that differences in prey type contributed to the coexistence of seven species of Asilidae, including two species of *Efferia*.

All three *Efferia* sp. foraged and fed more or less continuously throughout the day (Figs. 14, 15 and 16). However, they exhibited very little overlap in peak foraging periods. *Efferia cressoni* most actively foraged during mid-morning and early-evening; *E. subcuprea* foraged primarily during late-afternoon, and peak foraging for *E. triton* was during late-morning and late-afternoon. Differences in foraging peaks might also contribute to differences in prey selected. Such temporal partitioning might also eliminate opportunities for interspecific attacks.

Differences in prey selection also were reflected in predator prey ratios (Table 2). The three species fed on prey of different sizes, with the most noticeable difference being between *E. triton* and the other two species. *Efferia triton* fed on prey (\bar{x} 9.5 mm) which were approximately twice as large as those of *E. cressoni* (\bar{x} 4.6 mm) and 1.5 times as large as those of *E. subcuprea* (\bar{x} 6.1 mm). Dennis and Lavigne (1976) have indicated that partitioning of prey by size allowed for species coexistence in the species they studied.

Because *E. cressoni*, *E. subcuprea* and *E. triton* occupied different levels in the vegetation, observed contact between species was minimal. The latter species was the only one which was observed occasionally to prey on the other two species, presumably because of its intermediate level in the vegetation and larger size. Thus, it is assumed that competition for mates and the potential for interbreeding was reduced.

In summary, we speculate that, in combination, the aforementioned factors allow the three *Efferia* species to coexist. In addition to these factors, morphological differences and other behavioral adaptations as observed by Dennis and Lavigne (1976) also may contribute to the coexistence of these species.

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